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The correspondence between John Gerould and William Hovanitz and the evolution of the *Colias* hybridization problem (Lepidoptera: Pieridae)

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Abstract. The recently-discovered correspondence between Prof. John Gerould of Dartmouth College, who initiated the study of hybridization between sympatric North American species of *Colias*, and William Hovanitz, who made it the centerpiece of his research program in the 1940s and 50s, sheds light on the sources of Hovanitz's ideas and the evolving interpretation of that system, which remains a major challenge at the interface of population ecology and population genetics today.

Keywords: John Gerould, William Hovanitz, *Colias eurytheme, Colias eriphyle, Colias philodice*, interspecific hybridization, hybrid zone theory.

Introduction

Hybridization between sympatric North American species of the genus *Colias* Fabricius (Pieridae) remains one of the most vexing problems in the evolutionary ecology of butterflies and, more broadly, in our understanding of interspecific hybridization as a phenomenon. Hybridization between *C. eurytheme* Boisduval and *C. philodice* Godart *sensu lato* (now generally separated into two species: *C. philodice* in the East, and *C. eriphyle* Edwards in the West) has been studied since the 19th century in the West and since the advent of sympatry in the Mid-Atlantic States in the 1920s. Despite a very large bibliography (mostly cited in Jahner *et al.*, 2012), the phenomenon remains poorly understood. Basically, the question is as follows: wherever *C. eurytheme* is sympatric with one of the others, they hybridize, often at high frequency, yet they retain their separate identities and do not fuse. The "hybrid zone" includes virtually all of the continental United States except peninsular Florida and California west of the Sierra Nevada; and parts of southern Canada. Jahner *et al.* (2012) recently reviewed the situation historically and demonstrated, using path analysis, what factors seem to be the primary drivers of hybridization frequency at one locality which was sampled for 66 consecutive generations. They did not, however, identify the factor or factors keeping the populations distinct. Jahner *et al.* provide (partly as an Appendix) an historical retrospective on the study of hybridization in North American *Colias*, which is too large and complex a subject to reprise here. Both their paper and the Appendix can be obtained by e-mailing the author of this paper.

The two researchers who contributed the most to our understanding of *Colias* hybridization during the 20th century were Professor John Gerould of Dartmouth University and William Hovanitz. From their published works it is clear that Hovanitz derived inspiration from Gerould, but until a large, if incomplete, collection of their correspondence surfaced in 1993, it had not been known how frequent and detailed – and often contentious – their interchanges had been. Gerould's papers were deposited at Dartmouth after his death, and his library was sold off. Somehow the Hovanitz correspondence traveled with the library and ended up in the hands of an antiquarian bookseller, from whom I purchased it on December 9, 1993. The entire file will be donated to the Gerould archive at Dartmouth with the completion of this article. The letters, mostly originals from Hovanitz and saved carbon copies of Gerould's, begin in 1939 and continue through 1950. During the early part of the correspondence Hovanitz

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was a doctoral student at the California Institute of Technology under Nobel laureate Thomas Hunt Morgan and the also-distinguished A.H. Sturtevant. From 1943-1945 he had various assignments, largely focused on medical entomology, in South America, Michigan and Florida. He then studied with the ecologist Lee Dice at the University of Michigan before joining the faculty of Wayne State University in Detroit. His earliest *Colias* papers were based on research conducted as a graduate student and give his institutional affiliation as Cal Tech. Later productions emanated from Dice's Laboratory of Vertebrate Zoology at Ann Arbor and from Wayne. Miller (1979) published a bibliography of Hovanitz's publications.

The early Cal Tech period

Hovanitz's first letter to Gerould, dated September 17, 1939 – at the start of his first term in residence at the William G. Kerckhoff Laboratories in Pasadena – is of a sort very familiar to academics. It begins:

Dear Prof. Gerould:

For some time I have been interested in the variation of color in the scales of butterfly wings—especially as regards the relationship between ecologic habitat and the type of variation. Although as yet, I have not had the facilities for extensive experimentation, I hope in time (perhaps starting this winter with desert races) to be able to work on the physiology and genetics of color in the Nymphalidae...

He then sketches out a potential research program which would eventually be partially realized in his studies of parallel color variation in Melitaeini along climatic gradients. But he faces obstacles:

I would like to break the [larval] diapause and as I have found little in the literature of help, I wonder if you can help me with ideas? A second problem comes with mating. Though I have bred many insects, I have never tried to mate butterflies in captivity. Do you know any special way of accomplishing this?

In a handwritten PS, he asks for any available reprints on "butterfly genetics, etc." There is no mention of *Colias*. Clearly, Hovanitz did not have *Colias* in mind when he initiated contact. Presumably Gerould sent him reprints of his important *Colias* papers, which may account for the change in the thrust of Hovanitz's research which is evident a year later. Unfortunately, the beginning of his interest in *Colias* is lost. The next item in the file is from Hovanitz, dated Sept.10, 1940; by now he is deeply into *Colias* work, both in the field and the lab:

I wonder if you could get or know of someone who could get me some living material of Colias philodice. I am now breeding eurytheme and some of its Great Basin varieties which are intermediate between the two....

I am working on a curious population from near Mono Lake in Mono County, California. This is at an elevation of from 6500 feet up and the season is therefore short. In the spring (May and June) almost all the butterflies are pale yellow, like philodice, but as the season progresses orange forms become more and more abundant until in the fall (August and September) only orange forms are found. I have just bred out here in Pasadena over a hundred individuals obtained from the egg (three orange females laid them) and a good percentage are yellow. Yet the population from whence they came was at the time 100% orange (I counted 69 orange and 2 white).

He adds this handwritten PS:

The population above was obviously heterozygous for yellow (or rather, no orange) but what besides rather stringent seasonal selection could account for the lack of yellow at this time of year. All individuals bred were under identical environmental conditions.

Again, Gerould's reply is missing, but he wrote in longhand on Hovanitz's letter that he sent four female *philodice* to him Special Delivery (88c postage noted!—Gerould meticulously recorded such expenses and expected compensation) on Sept.23 and they had arrived OK and began laying. Gerould seems to have started keeping carbons of his letters only in early October.

Hovanitz's next letter is dated Sept.17, 1940. He thanks Gerould for his comments on his published paper about the Satyrids *Oeneis chryxus* Doubleday and *Oe. ivallda* Mead and discusses his hypotheses about the adaptive value of their coloration. A week later he sent a long letter, entirely in longhand. The first half is about parallel color variation in Melitaeini, but then it switches abruptly to *Colias* and one must regret the absence of Gerould's letter:

Your comments on the changing Colias population in the east is (*sic*) interesting. I do not think, though, that the population will change very much unless the climate and vegetative cover also changes more. I believe it is the removal of the forest cover over the east which has allowed eurytheme to encroach upon that territory. Over the dry hills of California, the form amphidusa never used to occur but it is now the commonest form because of irrigated alfalfa and clover fields. I am certain that environmental conditions had nothing to do with the color variation of the brood I spoke of....I am now mating the adults at 25C and breeding them all through the life cycle at 25C with a ten hour light day.

Humidity is kept at 80 though this is rather difficult in this place where it is normally closer to 0....Later, I will send you counts of the variations in the brood though this will be difficult because of the variation in the orange. The greenness of the underside varies as well.

The yellow butterflies from the brood above have difficulty in mating. As yet, I have gotten no fertile eggs from them....

I am of the opinion that eriphyle is nothing but the normal spring brood of the populations living between the Sierra Nevada and the Mississippi Valley.

In eastern Washington this is the case, in Modoc and Lassen counties, California this is the case. In the area from Mono Lake to the Owens Valley in Mono co., Calif. this is the case. All-year orange material is gotten only on the warm-winter western side... from B.C. to Mexico and east through Arizona and New Mexico so far as I know. Actually I do not consider them species hybrids but merely as individuals having, available or mixed in the population, genes for all the characters. Sterility seems to be a character not related to the color variation and present in distantly situated populations, but which is lost by sufficient inbreeding. Such sterile races seem to have gotten started and actually formed new species – for example, Colias hartfordi (*sic*) of California.... In geographically "isolated" strains where the distribution is continuous, I can only guess that an ecologic selection must keep the strains from completely mixing.

It is quite clear that Hovanitz is having trouble separating seasonal variation (polyphenism) from direct genetic color differences, and he is waffling over the same issues that troubled 19th-Century writers on *Colias*. He is ahead of his time in controlling the rearing environment strictly. The role of photoperiod in butterfly polyphenisms was completely unknown at this time; perhaps he got the idea it was relevant by encountering the then-current work on insect photoperiodism by Danilevskii in the Soviet Union.

He wrote again on Sept.26 to acknowledge receipt of the live *philodice*, which had taken only two days to cross the country. But then he writes three pages in longhand giving precise data on the reared Mono County brood, including wing color and size by sex and number of days egg to adult. Then:

My own opinion on the population here (which will probably go for all Great Basin ones above 5000' elevation in the south and sea level in the North) is that it is a continually fluctuating condition with regard to the genes which determine orange coloration. Judging from the geographical distribution of the Pieridae and the seasonal variations, I would expect that the individuals showing an increase in orange would be selected against over winter and in those areas which have colder winters. Thus there would be the factor of environmental conditions acting both upon the phenotype directly and also upon the hereditary constituents. The individuals manifesting orange certainly cannot pass the winter safely at Mono Lake because there is no orange there in the spring brood....With the increase in warm weather and warmer nights, the phenotypic and genotypic individuals would become more abundant....

The spring form from the coast of California has less orange than the summer form but never are all-yellow individuals obtained...

One is tempted to infer that his thinking here was colored by the just-published work of Timofeeff-Ressovsky (1940) on "cyclic polymorphism" in the ladybird beetle *Adalia*. As a graduate student in the Morgan lab he would definitely have known about it, whether or not he could read it in the original German.

Gerould replied in two parts, written on October 6 and 7. The first part concerns the invasion of the Northeast by *eurytheme*; he discounts "removal of forest cover" as a cause, says the species is non-migratory, and believes it has been accidentally introduced in commerce. In the second part he addresses the problem of *eriphyle:*

What you say about eriphyle interests me very much, for my experience with western yellow stocks east of the Rockies has not brought to light any seasonal change into orange. These stocks have been essentially true-breeding yellows, with a decided dash of orange on the under side of the forewings, distinguishing them from philodice. They mate readily with philodice, and I regard them and philodice as minor species sprung from the widely distributed eurytheme and segregated from it by partial sterility, like harfordi.

I have raised large broods of yellow Colorado, Alberta, Nebraska and Kansas stocks, all similar in some respects but different from one another particularly in the tone of the under side, which as you know is strongly subject to seasonal influences.

In the discussion that follows it is evident that Gerould has had Wyoming material of the *C. alexandra* W.H. Edwards complex confounded with *eriphyle*. This was presumably the fault of his supplier, but in any case it confuses the results. He is left uncertain of what *eriphyle* really is, biologically, and closes:

Your letters have been very stimulating and useful to me and I am very grateful to you for them.

Hovanitz wrote back at once (Oct.26). He noted that the Mono Lake population breeds on clovers, unlike pure *eurytheme* that "just swarms" over alfalfa; "automobiles on the highway become plastered with them." Much of the following discussion reflects uncertainty on the part of both men as to the true nature of *eriphyle, e.g.:*

I prefer to consider each population as a unit and not try to make any species differentiations in this group. I look as *(sic)* this group as a whole and then look at each part of it as an adaptive complex...

He then speculates on the adaptive value of wing pigmentation, drawing parallels to Melitaeines and *Oeneis*, and causing Gerould to draw large question marks in the margins next to his most speculative comments. After explaining the fundamentals of the Mediterranean climate of cismontane California (and getting parts of it wrong), Hovanitz attacks the question of why only oranges occur west of the Sierra but the situation to the east is so confusing:

East of this divide, winters are cold north of about latitude 37 and the populations are mixed with a yellow form that is abundant in the spring.

In Lassen County in July—late spring for there—the population was about 50% yellow and 50% orange. [Note: *Colias* fly in April in Lassen County, and Hovanitz was sampling the second generation.—AMS]

Yellows were in copulation with oranges. The same was true for

> Mono Lake in July. In late August as I wrote you the population was 100% orange phenotypically. Last weekend about 70 butterflies were captured and all were orange. This is the last for the season there as snow has fallen and the clover is dead.
>
> ...In the case of eriphyle I cannot consider the populations as specifically different from either philodice or eurytheme. They seem to be rather perfect intermediate blocks connecting the two, with the adaptive gene complex different from either.
>
> I am very grateful to you for your letters as one learns a great deal by discussing the problems. I am going to make periodic collections of material from Mono Lake next season (if Hitler doesn't come over!)and see if the seasonal selection of genes for orange- and yellow-colored forms has any truth in it.

Showing increasing impatience with Hovanitz's arm-waving, Gerould drew a big question mark at the phrase "seasonal selection." One wonders if he knew about Timofeeff-Ressovsky's work!

W.D. Field published his *Manual of the Butterflies of Kansas* in 1938, but apparently Hovanitz didn't read it until late in 1940. On Oct.29 he wrote Gerould that Field treats *philodice* and *eurytheme* as "subspecies" with *eriphyle* as a "form." But

> This, however, doesn't mean anything. What is interesting is the fact that eriphyle here seems to be two-brooded and does not interbreed enough with eurytheme to lose its identity. What more could be wanted for specific differentiation? I wonder if we don't have something here like the race A and B of Drosophila pseudoobscura at least in part [Note: these proved to be reproductively-isolated sibling species.—AMS]. Certainly, I believe the evidence of intergradation between some populations of the yellow form and the orange form is strong but in other cases, good physiological isolation seems to have developed.

On Nov.18 Hovanitz wrote that he would be on the East coast for a meeting and could be reached care of Theodosius Dobzhansky at Columbia University. Oh, to have heard their conversations!

Gerould replied on Nov.25 to Hovanitz's previous three communications. He offered to put up Hovanitz and his wife if they wanted to come for a visit. There is nothing to document whether this visit took place, as no more letters appear in the file until 1941. Most of this short communication is a dismissal of Hovanitz's suggestion that melanic coloration in *Colias* was adaptive in cold climates. He saw no mechanism for such adaptivity and thought melanism was an inevitable byproduct of slower metabolism at low temperatures. The adaptive value of seasonal polyphenism in *Colias* thermoregulation would not be demonstrated for another two decades, proving Hovanitz prescient. Hovanitz replied testily on New Year's Day, 1941 to a Gerould letter of Dec.22 that we do not have. The subject is still adaptive melanism, and he insists that the climatic correlations virtually demand an adaptive explanation: "I am sorry that we differ so greatly in this regard." He then goes on to reject some idea advanced by Gerould regarding recognizing backcrosses among the intermediates, but does not explain why.

At this point their correspondence seems decidedly strained. The next few letters concern rearing conditions and their impact on growth rates, survival and fertility; there is no talk of the *eriphyle* problem. Hovanitz sent Gerould a box of specimens to review. Gerould's notes on them are extant, but not a letter about them. The specimens were returned.

On May 20, 1941 Hovanitz wrote Gerould about discovering a new white mutant of *eurytheme,* perhaps homologous to either the "whitish" or "blonde" mutants later described by Remington in eastern *philodice.* Then he reports the first spring census at Mono Lake (mid-May) and exclaims:

> These results have decidedly surprised me and I'm afraid have thrown overboard my idea of seasonal selection, at least as supposed last year. Also, the overwintering of the orange and most white females is the only way I can account for these summer bred individuals (worn, too) at this time of year. I guess I have lots of surprises coming! Note the lack of the spring form of the orange type at least as it is known along the coast and the scarcity of white females in the spring emergence...

Hovanitz had fallen into the trap of assuming a single season of sampling would tell the full story. A perusal of the 66-generation record in Jahner *et al.* (2012) demonstrates the folly of single-year generalization. It is clear also that, just as he misread the seasonality in Lassen County, Hovanitz began sampling at Mono Lake a little later than he should have in 1941. Moreover, he was still missing the obvious solution to his problem: there is a routine upslope migration and colonization by *eurytheme* in late spring, a phenomenon fully documented at Sierra Valley by Jahner *et al.* The summer brood phenotypes of *eurytheme* that he censused in May 1941 had originated somewhere east and downslope of Mono Lake. By early July Hovanitz was reporting a ratio of 287 orange to 1 yellow female! In his letter of 20 July he announces discovery of a new population of yellows at Round Valley near Bishop, Inyo County (4500'). And for the first time he complains that his stocks are being ravaged by disease (presumably the classic *Colias* nuclear polyhedrosis virus, or "wilt disease"). We have no record of whether Gerould, who must have experienced virus problems also, had any useful advice, but during 1942 Hovanitz concluded that high water content of the food was a predisposing factor. He told Gerould he had largely overcome the problem by lowering the humidity in the rearing chambers.

During much of 1941 Hovanitz was preoccupied with seasonal variation in the frequency of white females. Gerould, on Nov.17, cautions that as far as he can determine, the white female form is completely genetic and not subject to direct environmental influences. On Nov.21 Hovanitz wrote that on the advice of Professor Sturtevant, he had begun doing sight counts of the color phases in the field and was reasonably convinced this would not introduce much error in the estimates of frequency. Gerould (December 1) begged to disagree,

> I am very skeptical about "counts," especially where the population is large. No human being can be quite sure whether any particular female has been seen by him already....Why adopt a very unreliable method when a perfectly reliable one (killing and preserving) is available and almost as convenient?

After a detailed discussion of the 1941 field data, his tone becomes quite harsh:

> I hope that you will pardon me for saying that I think it is a pity for you to publish these misleading data until you have checked them up next July. Entomologists would readily and thoughtlessly accept them as supporting their traditional belief that there is something seasonal (excess of whites in the fall) about the white female. This is pure bunk, pseudo-science, and I would hate to have to attack it in print.

This inspired a long letter from Hovanitz on Dec. 3rd.

> I am very sorry that my efforts to illustrate the variable ratio of white:orange females at Mono Lake has *(sic)* met with such violent repercussions. I think it will be noted that I have given no reason for the observed changes, nor do I harbor any....I do think that I have definitely shown a statistical and real change beyond that expected by random sampling alone. I do not know why they occurred....my abstract in Genetics states as much.

He goes on to review his field methods in detail, including a test involving mark-recapture [a method still quite novel in 1941] and adds:

> I agree with you that no one on earth can know if the butterflies I have counted have been counted once, twice, or many times. But that is not the point. Genetics is a science based on probabilities; I have shown by my marking experiments just what the probabilities are of capturing one once, twice, thrice etc. They follow the normal mathematical curve.
>
> If you intend to attack the traditional idea of entomologists that whites are of excess in the fall, I should prefer not to be mentioned since I do not believe in traditional ideas that are not based on fact, and I should not care to be misquoted.
>
> ....In conclusion, I feel safe to say that we both agree that what ideas are "pure bunk," "pseudoscience" etc. can only be proven or disproven by experiment or analysis. I should dislike very much to have you attack an analyzed case which I uphold as not "pure bunk" and have gone to great pains and expense to show is not.

This storm seems to have blown over, perhaps fading in significance in the wake of Pearl Harbor Day. There are no letters in the file until one from Gerould on Dec.22 concerning his treatment of *eriphyle* in a forthcoming paper (Gerould, 1943). In it he asks Hovanitz to fact-check his treatment of data derived from the latter's work, as well as the accuracy of quotes from their correspondence. He states that backcross phenotypes can be recognized, a prior point of contention. Hovanitz sent him 1941 specimens to examine in detail. In a letter of Jan. 12, 1942 he reports on his conclusions from that study and reaffirms his belief that backcrosses can be recognized, asking Hovanitz why he believes to the contrary. He also tells Hovanitz that he keeps carbon copies of typewritten letters and there is no need to return the originals. [If Hovanitz had been doing that, it makes the gaps in the file that much more mysterious.] Gerould says that the proportion of intermediate phenotypes is quite high in some Northeastern populations, prompting Hovanitz to say in his reply of Jan.26 that he had met with Austin Clark in the winter of 1940 and "it will be difficult to convince him of the interrelations between *eurytheme* and *eriphyle*." Clark (1932) had carefully documented the establishment of *eurytheme* in the vicinity of the District of Columbia after 1929 and was convinced that it was driving *philodice* to extinction there through hybridization; he called it the "persecution of one butterfly by another." But it is unclear why Hovanitz thought he would be resistant to his (Hovanitz's) story.

On Feb.8, 1942 Hovanitz wrote that the proportion of phenotypic *eurytheme-eriphyle* intermediates in Carson Valley, Nevada (Gardnerville, Minden, Carson City) is higher than of parentals! He does not say how many samples, taken over what period, might be at issue.

Most of a Feb. 26 Hovanitz letter is devoted to attempts to parse the transmission genetics of ground color. Results seemed to differ depending on the source of the parents, and the matter remained unresolved. This makes the issue of recognizing backcrosses moot, if one has no estimate of the number of loci involved and whether or not they are simply additive. Both men were fully competent geneticists. The issue has not been definitively resolved today, although for our group a model of two loci with no dominance and simple additivity seems to fit the lab brood distributions well. At the end he declares:

> Personally I do not think that there is specific differentiation (in a taxonomic sense) between philodice, eriphyle and eurytheme, though they are quite different in their physiological and genetic behavior. I do think that eriphyle has much more in common with philodice than with eurytheme (even besides color).

Gerould wrote "Correct" next to the last sentence. In his reply on March 10 he called that a "good letter," declaring that

When eriphyle is understood, then the hybridization problem can be approached with hope of success. Jumbling eriphyle with eurytheme, as one yellow-orange polymorphic species, would seem to me to be a concession to ignorance.

That paragraph could have been written before the entire correspondence had started! Had any meaningful progress been made toward clarifying the status of these entities?

The later Cal Tech period

March 20, 1942; Hovanitz felt he had turned a corner.

Our second term is now just finished, as is likewise the grind of getting over a few of the requirements for the degree. I feel a little relief over being past that and having ahead mainly the work with Colias.

All the past year I have felt chained down and unable to do what I wanted at the time it was most desirable. Now if the war does not interfere I shall be able to accomplish something (I hope).

Gerould had previously asked about white female *eriphyle,* and Hovanitz said he was not certain of their existence. Gerould replied on April 9 that his assumption that they did was based on treating yellows from Kansas as *eriphyle*—but now he was having second thoughts on the matter; perhaps they were really *philodice,* or intermediate. He wrote to Field about this on May 12, but Field's reply is not in the file. In his 1943 paper, Gerould referred to his Kansas stocks as *philodice,* explicitly declaring (p. 424) that after initially treating them as *eriphyle,* he had changed his mind.

The debate over sight vs. removal counting was again joined in May. On May 8 Hovanitz reiterated his preference for sight counts. But then he dropped a bombshell:

I expect to make quite a comprehensive analysis of the whole Colias problem in North America...if the war does not interfere by removing me too soon. Data from all the major museums of the U.S. is either here or coming and I have data from a very many private collections everywhere. I also have much data from eyewitnesses as to the increase of eurytheme throughout the east. On top of this, the breeding data which I am now really beginning to get is coming along....I have not yet been able to figure out a way of putting this mating behavior on a statistical basis, since the Drosophila system obviously won't work.

Gerould's reply is missing, but Hovanitz wrote on May 13:

I don't know what to say about the two pages you have sent me. There are a very many points with which I disagree but as yet can put up little really good proof. Making much at this stage of the game is hazardous and I think subject to too much later alterations....

Perhaps it would be better to leave my criticisms go for this paper unless you want them badly enough. My data and consequently my way of looking at these problems is changing all the time. There seems to be a decided "funny business" involved in the white female as well as the yellow and orange forms. I don't want to be pressed for an opinion at this stage of the game....I believe that I am just about to change my whole way of working at this problem and just when the light will dawn upon my at-present sleeping intellect, I don't know!

Again, Gerould's reply is missing. It is curious that Hovanitz retreated into declarations of uncertainty so quickly after announcing he was on the verge of a comprehensive synthesis!

On June 29 Hovanitz wrote to declare that he was now convinced [correctly] that the taxon *harfordi* (now spelled correctly) was a member of the *alexandra* group and irrelevant to the *eurytheme-eriphyle* story. On August 4, after a discussion of larval color and pattern in *Colias,* he declared:

I am discontinuing work on some of the stuff and soon will discontinue all but a mere line because of the war. I see little hope of staying out of the army beyond this fall or winter and there is no use being caught with too much on my hands. I wish that your paper were finished so that I could make a complete as possible job of Colias variation—geographical, genetical and environmental. The genetical part is going to be wholly inadequate at all events.

Gerould wrote in the margin that he had sent Hovanitz several sections of his own MS on Aug.11. Hovanitz returned from a field trip a week later and wrote that he had not had time to read the material. But as for his own plans, he was still wavering:

Perhaps I should, however, correct or modify the impression that I gave in my last letter, namely, that I was giving everything up. On the contrary, I fully expect to get my material in shape and to turn it in as a thesis. I had in mind before only the discontinuance of the hybridization problem. My F1 and backcrosses have given my *(sic)* data which suggests in which direction I should work to carry out the analysis further. However this would entail too much work and preparation for the time possibly available. I have come to definite conclusions concerning the interrelations of eriphyle and eurytheme,and the status of the intermediates in tbe populations. I don't think they will be entirely the same as yours....I see no reason why I should notpublish my data; I believe I have enough now to make a small monograph! (Including the complete geographical distribution and speciation in North America.)

There is not another letter from Gerould in the file until May 4, 1943. But there is a steady stream from Hovanitz.

On August 19, 1942 Hovanitz commented on Gerould's manuscript:

The conclusion that eriphyle is something genetically distinct from eurytheme, which you come to in your paper is the point that I have been trying to solve for these two years. Fortunately, we both come to the same conclusion. Unfortunately, I was not aware that you would or had come to the conclusion and hence one of the points upon which my thesis is based is a little exploded! I do not know what your complete data is on eriphyle. The complete tale is far from being told even with my data but as I said I think that I had better stop the work now. I believe that my analysis of the two populations (Mono Lake and Round Valley) for 1941-42 and other populations elsewhere for white female frequency plus the genetic and physiologic data obtained should suffice [for the thesis]. Besides as I believe I have already stated I have made a complete study of the geographic distribution and variation of the forms throughout North and Central America and therefore can come to very definite conclusions as to the probable origins, migrations, ecology, hybridization of the forms. There are some genetic and physiologic questions related to the hybridization which I should have liked to have answered but the data of neither of us is complete enough for that....

It would be highly convenient if I might be able to have a copy of your manuscript when it is completed or whenever you can spare one, since I had intended to cover the literature on this subject. I note that you are covering a good deal of it in the pages you have sent me and it would save needless duplication to know how much you are covering.

There is no indication that Gerould sent any additional material in reply to this letter, but Hovanitz wrote again on September 1:

I do not think that your data is any more significant that eriphyle is a species than Edwards' was that it is not. Surely it breeds true but so do thousands of genetic mutants in Drosophila but certainly species are not made this way. I must say that from what I know at present of your data, that your conclusions do not have any stronger foundation than that of the taxonomist who knows the animal in the museum and field....

I have been working on the point from the geographical distribution, the genetic, the ecologic, physiologic, etc. points of view and have a tremendous lot of data to show its status. Still I have not made up my mind whether to call it a species or not. I rather think that I shall not.

I should abhor coming to the conclusion in print that I do not think your data are significant. Surely if I were in your place I would not come to a definite conclusion—to do so is identical to doing as a normal taxonomist does who "feels" what a species and subspecies is. I am sorry that I have to say this because I believe your work is important and represents a lot of effort. Taxonomists, however, are likely to view with skepticism the conclusions of geneticists...

And the very next day:

I hope that you will excuse my writing so much about whether I consider eriphyle a species or not... Recently I gave a talk in Berkeley and, pressed for a statement on this point, I said that you could flip a coin and take your pick that way. Of course it isn't as simple as that but I have just now decided that I find it more convenient and my paper much clearer if I don't come to any conclusion of that sort. Instead, I shall segregate my material in discussion to orange form and yellow form. Therefore I shall not object to your usage though I myself dislike calling them species and your usage of the term hybrid.

Apparently Gerould sent the complete text as it stood at that time, prompting a reply from Hovanitz on September 9:

You are truly kind to send me the copy of your manuscript even after the way I have written.—I am very sorry that I cannot say that my opinions have changed since reading it, in fact they have become more definite. —This thing has placed me in a very bad spot and I don't know what to do. I can't possibly agree with you on your ideas of geographical distribution—they are based upon such skimpy data.

Yet if there is anyone I want more to agree with it is with you. To tell the truth which is not to be public information, I feel in about the same position as Sturtevant now is in with respect to Patterson on Drosophila species.

It is from data from everywhere that a ...general view of the problem [can be] obtained. ..Flops such as are being made daily on species problems or evolution treatises would not be made if persons would not be so narrow in their viewpoints....

I love arguments but I don't like the strained feelings that so often accompany them. As this is perhaps my last chance to write up a bit of work before going into war service, and perhaps the last of my work on butterflies, I think that it is fair to state my opinions on the problem. My general type of consideration will be clear from my last paper now in press in The American Naturalist on the "Geographical distribution and racial structure of Argynnis callippe in California and Nevada"....My method is to eliminate orthodoxy in geographical distribution work...

Don't misunderstand me. I think your paper excellent with the exception of the one point discussed so much...If I did not recognize its worth I would not mention it twice or even criticize it.

Hoping for the best,

Gerould's letter of Sept.18, referred to in Hovanitz's of Sept.25, is very unfortunately not present.

I am most grateful for your very long and excellent letter of Sept. 18, 1942.

Hovanitz revealed that he had received a six-month draft deferment to complete his work. He will concentrate on the white-female problem. The next day he wrote again with an urgent request, with just a hint of panic:

I trust that you will keep my work on these problems confidential and that you realize how important it is to me that this work remain original with me. Not having known how much you did on the yellow x orange crosses, I made unnecessary duplications. Many of the statements I make in my letters are based upon tedious research, likewise, the questions I ask, and it is very hard to see these things published before I have had the chance to present the evidence, at which time it has but second-hand value. You will, I trust, be considerate of this because I have been so willing to discuss with you all the time the results of my work as it has progressed.

On Jan. 29, 1943, Hovanitz wrote that all the formalities for his degree had been completed except filing the thesis; that he had accepted a commission as an entomologist in the Armed Forces; and that, preparatory to publishing his research, he had prepared a "short paper reorganizing the nomenclature of the group." Would Gerould review it? The MS is not in the file, but Gerould did comment on it. This MS, subsequently published (1943) in the American Museum Novitates, was apparently the first place where Hovanitz, employing his announced view to global distributions, adopted a proposal by Austin Clark and combined the North American taxa *eurytheme, eriphyle* and *philodice* under the Palearctic taxon *chrysotheme* Esper, an action which when actually published was to be ignored by virtually all taxonomists—although it foreshadowed a wave of Holarctic lumping in butterfly nomenclature some thirty years later, which sunk a number of Nearctic taxa as subspecies of their (nomenclatorially older) Palearctic relatives. Hovanitz wrote a lengthy rejoinder to Gerould's (missing) critique, Feb.5, 1943:

I am exceedingly grateful for your notes and comments on my paper. It is by the fair interexchange of ideas that science may profit. Nomenclature has two functions to perform—it must be convenient to use and should show as best as possible the relationships between things. I agree with you that chrysotheme is not the best name to use for the purpose in which I have used it. But neither eurytheme nor philodice is as satisfactory. Likewise I do not feel that a new name should be formed for this purpose, and therefore I have chosen the one least apt to form confusion. The chances are great that the morphological similarity between the Palearctic forms and the Nearctic forms will be justified in genetic similarity when breeding tests are made. If not, a change must be made. In how many living things have genetic tests been possible?...

Unfortunately, I do not feel that the nature of the case justifies the rash statements made with respect to my judgment...I have covered the literature and the museums of America. I have had genetic and ecologic experience with all these forms...a total of over 6000 museum specimens, a total of over 50,000 sampled individuals in California...I have bred the material as you have and I must say I appreciate the fact that you are the only other person beside myself who has done so. I will admit that Clark has not gone into great geographical detail but who has but myself on this group? I must assume that "snap judgments" as you put it must apply to all, then. Certainly the snap judgments of Edwards made years ago when little was known cannot be held forever....

Your geographical data and theories, with which I did not agree, are not the main part of your paper. Your genetic results are very accurate and good. They agree with mine and this is the main part....

I have an entirely different idea in the main point of difference between the orange and yellow races from what you apparently have. This is very briefly abstracted in the December number of the Bulletin of the Ecological Society of America 1942. Again, how can I make any comments on your work? There is nothing I find wrong with it but nonetheless I derive different conclusions on the basis of additional information. I admit and deeply acknowledge the fact that I could never have arrived at these conclusions if I had not had your earlier work....Surely it is not expected of scientists to maintain their original conclusions despite the advances in the science...It is seldom that I have found reason to question this faith I have had in you [to be objective].

Gerould wrote a rebuttal to this letter. For some reason he kept a rough draft of that rebuttal, although the finished letter is missing. From Gerould's draft, dated Feb.8:

I had no intention of attributing a "snap judgment" to you, but rather to Mr. Clark whose proposed nomenclature you seemed to be adopting. If you must lump these American orange and yellow species and subspecies together, as you seem bound to do as the result of your extensive studies, you need, as you say, one name. W.D. Field in '38 used philodice Godart. Field speaks of C. philodice eurytheme. Evidently you don't like that plan any better than I do, nor do you like C. eurytheme, coined later. If you must have trinomials, that is the name I should choose rather than the very little-studied European-Asiatic chrysotheme. Have you personally studied the morphology of chrysotheme in any way corresponding to the exhaustive studies you have devoted to the American forms?

He also took Hovanitz to task for using the word "data" as both singular and plural, and for errors in his use of Latin!

Hovanitz replied three days later, Feb. 11th.

Since we agree on the fundamentals of the Colias problem, does it not seem like a lot of unnecessary quibbling to argue about names? Names are only a means to an end. They are of use only so that we may know what we are talking about. If I used philodice as a name for all the N.A. forms or eurytheme for the same purpose, the restrictions which people have in their minds to each of these would be too difficult to overcome. Chrysotheme is admittedly not too logical but for the time being it is practical.

Colias lesbia of Argentina is nearly identical with eurytheme of North America. It has the same seasonal forms, the same habits, the same food-plant preferences. It is as much a pest on alfalfa in that region as eurytheme is in California. I would be tempted to classify lesbia with eurytheme and chrysotheme. ...It was to avoid unnecessary quibbling about names that I dropped out of taxonomy in the strict sense a long time ago.

On April 4 Hovanitz sent Gerould a genetics manuscript. Gerould's reply, as usual, is missing, but Hovanitz wrote a long response dated April 24. Most of the content is detailed and requires reference to the MS to be fully understood, but there is a trenchant comment on names again:

As far as the entomologists are concerned, I have not paid any attention to their nomenclatorial arguments of which there are many in the 19th Century. Personally, I think you have overrated the value of the statements of the 19th *(sic)* entomologists and have partially succumbed to their style of argument or "hunches."...Your play on names throughout [your] paper is an old taxonomists' trick which serves only to cover the true facts and relationships in this group.

The file contains a second Hovanitz letter also dated April 24.

Certainly, collectors in the field seem to know more about the true situation than anyone, whether a taxonomist in Ottawa, Ithaca, or Washington, or a geneticist in Hanover or Pasadena.

....I have found it necessary to ignore the statements which you have made. No field man is going to be able to reconcile his field knowledge with the statements you have made...May I ask, since I do not have your full paper, just what is the basis for your conclusion "that eriphyle of Pueblo, Colo is of an independent true-breeding minor species, as I have found it to be the case at other western localities?" ..."Breeding true" is a slim excuse for a "species." Since eriphyle is to you a minor species and eurytheme and philodice are major species, what is your definition of "major" and "minor" species?

Suddenly we have a carbon of Gerould's 5-page reply, dated May 4.

> Instead of regarding our American "chrysotheme" as one huge "species," as Clark and you do, I am more interested in a genetic approach to its evolution, in the integrity of its races and their physiological relations to one another. So long as your conception does not run counter to the facts as I have found them, I have no quarrel with it. ...So I still speak of the "eriphyle-philodice complex" as split off from eurytheme....
>
> How it [this group] got that way [so confusing] recently near Washington, D.C. should be evident to Austin Clark, though, disliking "hybridization," he revises the taxonomy and tries lumping. I had a good talk with him the last time I was in Washington. He knew everything about Colias. I admire his brilliance more than I trust his judgment and I like him personally.

Hovanitz wrote rather contritely on May 9 after reading this long epistle:

> I have been thinking about the statements which you have made in your paper concerning the work of Scudder, Edwards etc. and believe that perhaps I have criticized [them] too harshly...

And even more contritely on May 14.

> Your long letter of May 4 is appreciated and surely shows that the attitude I took in my previous letters was wholly unwarranted

But then Gerould's big 1943 paper came out. Hovanitz, August 13:

> Although I like your paper very much I am sorry you went into points such as the distribution of the races, etc. that you knew I was going to cover thoroughly. I did not see these parts in your original manuscript. For this reason, I cannot help duplicating some of the portions in your paper, though I believe priority on my part was warranted here. You have been very fair in citing me in several places but I cannot help feel that many portions of your manuscript were written with my results in mind. I do feel that I have been fair with you in withholding publication of my data and in my citation of your data. You have certainly been kind in allowing me the prepublication use of the latter. It would have been nice had we been able to pool our data and make a really better work out of the whole, but I guess our differences are rather great...Monday, Aug. 16 I leave for Colombia [to work on mosquito genetics]...

Although the two men would remain in intermittent contact, the intense part of their relationship was over, and the enigmatic entity *eriphyle* would never be mentioned in their correspondence again.

After Cal Tech

Hovanitz continued to write to Gerould from Colombia. His initial letters were strictly descriptive (Gerould had never been to South America) and did not refer to *Colias* at all. Gerould apparently took the August 13 letter well, since Hovanitz opens his October 19 missive from Villavicencio thus:

> Your attitude on my last letter from Pasadena is of such a nature that I cannot help but comment on it. Were more scientific people of your type I am sure the world would get along famously. You are certainly of the true scientific spirit...It is, I am finding, very difficult to find people with a fair and reasonable attitude such as yours.

On November 1 Gerould wrote to inquire if Hovanitz had found any *Colias* in Colombia. He mentioned that Austin Clark had failed to get him a series demonstrating the alleged absorption of *philodice* by *eurytheme* in the D.C. area, and that there was a large "false brood" of *Colias* at Hanover, N.H. on November 1 that included both species and a putative hybrid. Hovanitz replied on December 7 that he was rearing the Andean *C. dimera* Doubleday on clover. Having returned to the States, he reestablished contact in a letter from Tallahassee, Fl, October 3, 1944. in it he mentions hearing from William T.M. Forbes to the effect that the oldest records of *eurytheme* in the Northeast were under Palearctic species names (a common early mistake!) and had been missed, thereby creating a false impression of its absence there. On Nov.11, 1944, writing from the Rockefeller Foundation in New York, he notes the occurrence of a "false brood" there and discusses the previously-commented-upon tendency of half-grown larvae of *philodice* to enter diapause while *eurytheme* does not. After 1944 the letters become quite infrequent. By spring, 1945 Hovanitz is ensconced in Lee Dice's lab at the University of Michigan and tells Gerould he can hardly wait to see what *Colias* are up to. This initiates a new round of correspondence, with Hovanitz sending Gerould field data and observations, and Gerould commenting thereupon, all in a genial manner—except for occasional digs by Gerould at what he still sees as the folly of lumping everything into *chrysotheme*. There is further discussion of whether or not there is a latitudinal and/or seasonal gradient in the frequency of white females. In 1947 Hovanitz went to the Arctic under the aegis of the Arctic Institute of North America to study *Colias* there and furnished Gerould a copy of his progress report, "Analysis of Natural Hybridization and Gene Frequencies in Arctic and Subarctic *Colias* butterflies." A second progress report was produced in 1948. Some of the publication from this work was delayed many years.

By 1950 Hovanitz was at the University of San Francisco and Gerould was working on his behalf to try to secure funding for *Colias* research, possibly in collaboration with Bjorn Petersen in Sweden, who had published recently in the journal *Evolution*. The last item in the file is a handwritten note from Gerould to Hovanitz about this, dated January 30, 1950. Gerould died in 1961 at the age of 93. Hovanitz died in 1977 at the age of 62.

Coda

Reading the classic *Colias* papers of both men demonstrates inconsistencies in their points of view but hardly reveals the drama of their highly fraught relationship, especially during the latter half of Hovanitz's graduate studies when he became increasingly apprehensive about competition for priority. Having initiated the epistolary relationship with Gerould – initially not about *Colias* at all! – Hovanitz apparently came to believe he had told the older man too much of his thinking. At the same time, he could not restrain himself at times and would lash out intemperately at Gerould, only to backtrack and more or less apologize. Gerould, for his part, must have realized by some time in 1941 that Hovanitz was not just an acolyte, but a potential rival for "ownership" of the system. Having carried out breeding experiments over decades on an opportunistic basis, he clearly perceived a need to bring them together into one or more major publications – and soon. The perceived threat seems to affect his tone. He could be picky and a bit patronizing, and even brutal in his criticism ("bunk", "pseudoscience") but also seems to have accepted Hovanitz's apologies graciously. It is very unfortunate that some key letters are missing. How, for example, did Gerould defend his terms "minor species" and "major species" when called on them by Hovanitz? These terms were never adopted by any significant number of evolutionary biologists.

A noteworthy aspect of the correspondence is the lack of any discussion of the "reinforcement model" of speciation. The idea that selection against hybrids could lead to the deepening of prezygotic reproductive isolating mechanisms, and thus to the "completion" of speciation, had been entertained by Alfred Russel Wallace, but was explicitly advanced by Fisher (1930) in his *Genetical Theory of Natural Selection* and by Dobzhansky (1941) in *Genetics and the Origin of Species*. Both books would have been well-known to both men, and Dobzhansky's would have been read avidly in the genetics group at Cal Tech even as these discussions went forward. Reinforcement would seem to be potentially highly relevant to the conundrum of *eriphyle*, as well as the recent sympatry in the East. (Klots, in his field guide (1961), actually alluded to this in his discussion of *Colias*.) If *eurytheme* and *philodice/eriphyle* are indeed species, why do we not see selection at work to deepen prezygotic reproductive isolating mechanisms between them? How could two species hybridize everywhere they came into contact and neither fuse together nor develop reproductive isolation, the two alternatives posited by neo-Darwinian theory? The discussions in these letters, like the papers, are highly taxon-specific and phenomenological and break no new theoretical ground; neither the Fisher nor the Dobzhansky book is cited in any of the papers from this period. The most theoretical treatment of *Colias* by Gerould was in a very early paper (1914) on mechanisms of speciation. Perhaps both men at this point subscribed to Muller's (1940, 1942) belief that reproductive isolating mechanisms arose incidentally to selection for physiological traits. This would not be surprising for Gerould; it would be much more surprising for Hovanitz. But Muller is not cited either. Nor did the extensive literature of apparently stable hybridization in plants come under scrutiny, despite the fact that with reference to hybridization, *Colias* act more like plants than animals normally do. The bibliographies of the *Colias* papers are remarkably parochial, given that the work was being performed at a time of intense and highly productive ferment in evolutionary biology and that both men had entrée to that ferment.

Both men were somewhat resistant to the ideas of the other, even when the matters that separated them in retrospect seem rather trivial. The only idea that seems to have disappeared entirely during their exchange was Hovanitz's of alternating seasonal selection, which was derived from a single season's observations at the very beginning of his career, and as noted may have been derivative from a current case of this sort in the literature. (The entire history examined here forcefully demonstrates the folly of hasty generalization from a handful of cases; Hovanitz was right in urging a broader view, though the geographic perspective he embraced was decidedly premature and seemingly "hyped" in his rhetoric.) Both men repeatedly circled the species question very warily. In this regard their genetic data should have given them an advantage over the 19th century entomologists disparaged by Hovanitz but taken seriously by Gerould. But they didn't, because there were no clear genetic criteria for deciding the question of speciation.

The factors maintaining the apparent equilibrium of hybridization in mixed *Colias* populations remain almost as murky as they were in 1950. The lack of introgression documented by Jahner *et al.* (2012) at Sierra Valley appears typical, but why? Why does larval diapause consistently fail to introgress into *eurytheme*, as noted by both Gerould and Hovanitz as well as by Jahner *et al.*? In retrospect it seems that these two men took the system about as far as it could be taken in their time. It is remarkable that so few observations have been made of the situation in the field (none in eastern California between 1943 and 1981!) and that the pattern of spatial and seasonal occurrence of hybridization remains so very poorly documented. Many more such data are needed, but they will have to be combined with cutting-edge genomic analysis if we are ever to crack the enigma of *Colias*.

Acknowledgements

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